Chromosome numbers of some Acanthaceae from Papua New Guinea

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Summary

Daniel, Thomas F. (2000). Chromosome numbers of some Acanthaceae from Papua New Guinea. *Austrobaileya* 5(4): 651–659. Meiotic chromosome numbers are reported for nine species representing eight genera of Acanthaceae from Madang and Morobe provinces in Papua New Guinea. Chromosome numbers of five species are reported for the first time and two new numbers are reported for the widely cultivated species *Graptophyllum pictum* (L.) Griff. Chromosome numbers obtained in *Calycacanthus* K.Schum. (n = 16) and *Jadunia* Lindau (n = ca 16) are the first reported for these genera. Subfamilial relationships are discussed with respect to the chromosome numbers now known for these and other Acanthaceae.

Keywords: Acanthaceae, chromosomes, Papua New Guinea, *Aphelandra*, *Calycacanthus*, *Graptophyllum*, *Hypoestes*, *Jadunia*, *Lepidagathis*, *Ruellia*, *Thunbergia* .

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Introduction

The pantropical family Acanthaceae comprise more than 4000 species in some 230 genera. Major concentrations of species occur in the following regions: Mexico-Central America, Andean South America, Brazil, tropical Africa, Madagascar, India, southeastern mainland Asia, and insular Malesia. Two subfamilial classifications of Acanthaceae are currently in use. That of Lindau (1895) includes all genera of the family recognized up to its publication but is now largely out of date and contains many errors. Bremekamp's 1965 revised classification made some improvements on Lindau's, but did not assign all genera to suprageneric taxa. An updated subfamilial classification, based on both morphological and DNA sequence data, is being formulated (e.g., McDade et al. 2000, Manktelow et al. in review, McDade et al. submitted).

Like many large and predominantly tropical families of flowering plants, the Acanthaceae remain relatively little-studied cytologically. In 1982, Saggoo and Bir reported that chromosome numbers had been determined for only about 219 species in the family, and Daniel and Chuang (1998) noted that only 62 of the 228 genera of Acanthaceae (i.e., 27%) recognized in Brummitt (1992) have received any cytological investigation. Whereas Acanthaceae occurring in India and Mexico-Central America have received the most cytological attention, those in Madagascar and insular Malesia have received little, if any, such studies. Barker (1986) noted that no cytological studies had been carried out on Australian species either.

In 1992, I had the opportunity to collect cytological samples of Acanthaceae in Papua New Guinea. Chromosome number determinations based on acanthaceous plants growing in Papuasia had not previously been made. In the discussions that follow, Papuasia refers to New Guinea and the Solomon Islands; New Guinea refers to the nation of Papua New Guinea (including the archipelagos of New Britain and New Ireland) and the province of Irian Jaya of the nation of Indonesia. Höft (1992) recognized 129 species in 30 genera (incorrectly totaled as 32) of Acanthaceae in Papuasia. At least 23 of these genera are native and four of them are endemic there. Unfortunately, there is no comprehensive systematic treatment of the Acanthaceae of either Papuasia or the Malesian region. The recognition of 129 species of the family in Papuasia by Höft (1992) is likely a

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conservative estimate; for example, the genus of at least one species that I observed as naturalized in Papua New Guinea (*Blechum pyramidatum* (Lam.) Urb.) was not listed by Höft. For comparison, about 60 species of Acanthaceae have been recognized from Australia (Barker 1986, 1996), about 160 (including many cultivated ornamentals) were treated as occurring in Java (Backer and Bakhuizen van den Brink 1965), and 168 were recognized earlier this century on the Malay Peninsula (Ridley 1923).

In this study, meiotic chromosome numbers are reported for nine species of Acanthaceae occurring in Papua New Guinea (Table 1). Six of these species (*Calycacanthus magnusianus* K.Schum., *Graptophyllum pictum* (L.) Griff., *Hypoestes floribunda* R.Br., *Jadunia biroi* (Lindau & K.Schum.) Lindau, *Lepidagathis royenii* Bremek., and *Ruellia repens* L.) are indigenous to the region, three (*C. magnusianus*, *G. pictum*, and *J. biroi*) are presumed to be endemic there, and three (*Aphelandra sinclairiana* Nees, *Ruellia tuberosa* L., and *Thunbergia grandiflora* Roxb.) are naturalized introductions. Chromosome counts have been reported previously for at least 20 acanthaceous species that occur in Papuasia. None of these counts, with the probable exception of *Graptophyllum pictum* (see discussion below), was based on plants from New Guinea or the Solomon Islands. They encompass either widespread species that occur indigenously in Papuasia (e.g., *Acanthus ilicifolius* L.) or species that are native elsewhere but which have become naturalized in Papuasia (e.g., *Ruellia tuberosa*).

Materials and Methods

During July and August of 1992, buds, seeds, and herbarium vouchers of Acanthaceae were collected in Madang and Morobe provinces of northeastern Papua New Guinea. Other Acanthaceae were grown in a greenhouse in San Francisco from seed collected in Madang province. Voucher specimens of the latter were made from the cultivated plants and the letters "gh" follow the field-collection numbers for them. Floral buds for chromosomal studies were fixed in absolute ethanol:glacial acetic acid (3:1) for 24 hours and subsequently washed and stored in 70% ethanol until processed. Anthers were macerated in 1% ferric acetocarmine and subsequently squashed on a microscope slide. Chromosomes were studied under oil immersion using a phase contrast microscope at a magnification of 1000x. Counts from at least two cells were made for most collections and all counts were verified by at least three persons. Camera lucida drawings were made of preparations from which counts were obtained. Voucher specimens are deposited at CAS and LAE. Camera lucida drawings are attached to the vouchers at CAS. Representative drawings for each of the species native to Papua New Guinea are illustrated. In the following discussions, all previously published chromosome counts are listed as *n* numbers irrespective of whether they were originally reported as sporophytic or gametophytic numbers. Voucher specimens, if they exist, that document previous counts by other workers have not been examined.

Results and Discussion

Chromosome numbers obtained from these studies are summarized in Table 1. The significance of each count is presented in the following discussions of the genera studied.

Aphelandra R.Br.

Aphelandra is a neotropical genus of about 175 species. The genus is represented in New Guinea by *A. sinclairiana* Nees, a native of southern Central America. This showy species with orange bracts and large, pink corollas is sometimes cultivated for ornament and has become naturalized in Madang Province. Our count of $n = 14$ for this species agrees with previously published counts for it based on plants from neotropical habitats (McDade 1984). This number is also the most widely known number in *Aphelandra* and likely represents the basic number for the genus (Daniel et al. 1990). Close relatives of *Aphelandra* in Lindau's (1895) Aphelandreae (i.e., *Holographis* Nees and *Stenandrium* Nees) both appear to have a basic number of = 13 (Daniel et al. 1984, 1990; Piovano and Bernardello 1991)

Table 1. Meiotic chromosome numbers of someAcanthaceae from Papua New Guinea.

Species	*n*	Voucher
Aphelandra sinclairiana	14	Madang: Daniel & Forster 6523
Calycacanthus magnusianus	16	Madang: Daniel & Jebb 6518
Graptophyllum pictum	21	Madang: Daniel et al. 6525
G. pictum	20	Madang: Daniel et al. 6530
G. pictum	ca 20	Madang: Daniel 6611
G. pictum	21	Madang: Daniel 6624
Hypoestes floribunda	15	Madang: Daniel et al. 6551
Jadunia biroi	ca 16	Morobe: Daniel et al. 6603
Lepidagathis royenii	21	Madang: Daniel & Forster 6522
L. royenii	ca 21	Madang: Daniel et al. 6538
L. royenii	21	Madang: Daniel et al. 6607
L. royenii	ca 21	Madang: Daniel et al. 6609
Ruellia repens	12	Madang: Daniel 6610gh
Ruellia tuberosa	17	Madang: Daniel 6626gh
Thunbergia grandiflora	28	Madang: Daniel 6627

Several authors have suggested that $x = 7$ is primitive for Acanthaceae (Grant 1955; Raven 1975; Piovano and Bernardello 1991; Daniel and Chuang 1993). If so, $x = 14$ likely represents a tetraploid derivative of this primitive basic number, and $x = 13$ has evolved via both polyploidy and dysploidy.

Calycacanthus K.Schum.

Calycacanthus is a unispecific genus endemic to Papuasia. The count of $n = 16$ (Fig. 1) for *C. magnusianus* is the first report of a chromosome number in the genus. *Calycacanthus* was included in tribe Odontonemeae subtribe Odontoneminae by Lindau (1895) and would be included in Bremekamp's (1965) tribe Justicieae subtribe Odontoneminae. Chromosome numbers reported for other genera of Lindau's subtribe comprise $n = 11$, 12, 14, 22, 23, and 28 (for *Siphonoglossa* Oerst., now treated as congeneric with *Justicia* L. of subtribe Justiciinae); $n = 15$ (for *Rhinacanthus* Nees, a genus best treated in subtribe Justiciinae according to Daniel and Chuang, 1998; for information on a dubious and unconfirmable report of $n = 16$ in this genus, see Daniel and Chuang, 1998); $n = 18$ (for *Streblacanthus* Kuntze and *Razisea* Oerst., the latter best treated in subtribe Isoglossinae according to Daniel, 1999); $n = 20$ (for *Ecbolium* Kurz); $n = 21$ (for *Odontonema* Nees, *Oplonia* Raf., and *Pseuderanthemum* Radlk.); and $n = 42$ (for *Mackaya* Harvey). Thus, $n = 16$ is newly reported for the subtribe as delimited by Lindau (1895).

Graptophyllum Nees.

Graptophyllum comprises between 10 and 15 species occurring primarily in the southwestern Pacific region. Barker (1986) noted three species in New Guinea whereas Höft (1992) listed five as occurring in Papuasia. The only previous reports of chromosome numbers in the genus are for the widely cultivated species *G. pictum* (L.) Griff., which has been reported to have been probably derived from Papuasian plants (e.g., Bailey 1949, Barker 1986). My counts from wild population of this species do not agree with previous reports for it, all of which appear to have been based on cultivated plants. Grant (1955) and Govindarajan and Subramanian (1983, without citation of voucher) reported $n = 30$ and Lakshmi and Bapa Rao (1977, without citation of voucher) reported $n = 18$ for *G. pictum*.

Fig 1. Camera lucida drawings of meiotic chromosome preparation. ***Calycacanthus magnusianus*** (*Daniel & Jebb* 6518), metaphase I, n = 16.

During my studies, chromosome counts were obtained from several cells at various stages of meiosis in each of *Daniel* 6624 (n = 21), *Daniel* 6525 (n = 21, Fig. 2A), and *Daniel* 6530 (n = 20, Fig. 2B). Similar differences in meiotic chromosome numbers among different collections of the same taxon are uncommon but not without precedent in the Acanthaceae. For example, both n = 11 and n = 12 have been reported for *Elytraria imbricata* (Vahl) Pers. (Daniel et al. 1990) and *Siphonoglossa ramosa* Oerst. (Hilsenbeck 1983), and both n = 22 and n = 23 have been reported for *S. sessilis* (Jacq.) Oerst. (Hilsenbeck 1983). The single cell with nearly countable chromosomes in *Daniel 6611* can only be estimated to be n = ca 20 because of dark cytoplasmic staining, overlapping of the irregularly shaped chromosomes, and the presence of dark granules.

Lindau (1895) included *Graptophyllum* in his tribe Graptophylleae along with a diverse array of other genera, many of which subsequently have been shown to be more closely related to genera in other tribes. *Graptophyllum* is similar in numerous morphological features (e.g., presence of staminodes, pollen type) to *Pseuderanthemum* and its relatives (see Daniel 1995). This latter assemblage also shares a chromosome number of n = 21. Based on numbers so far reported for *G. pictum*, a basic number of x = 10 is suggested for *Graptophyllum*; however,

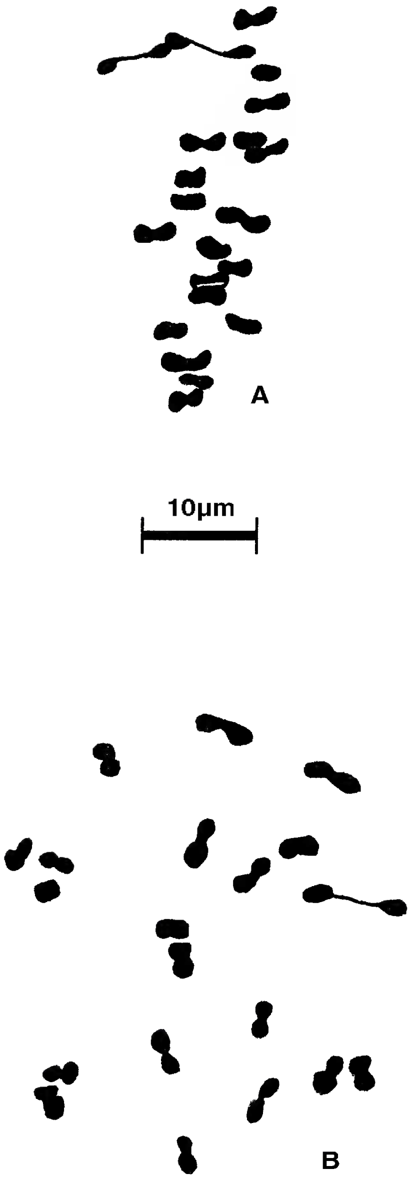

Fig 2. Camera lucida drawings of meiotic chromosome preparation. A.***Graptophyllum pictum*** (*Daniel* et al. 6525), metaphase I, n = 21. B. ***G. pictum*** (*Daniel* et al. 6530), metaphase I, n = 20.

this number is not currently known in the genus. Determinations of chromosome numbers for other species of *Graptophyllum* will be necessary in order to confirm this or establish another number as basic in the genus.

Graptophyllum pictum has long been assumed to be native, and probably endemic, to New Guinea (see discussion by Barker 1986). My collections of the species from forest habitats in Papua New Guinea differ from cultivated plants (based on collections from Hawaii, Panama, Papua New Guinea, and the West Indies at CAS) by lacking variegated coloring in the leaves, having narrower (less than 1 mm wide vs. usually more than 1 mm wide) and more attenuate calyx lobes, and having fruits present. The cytological and morphological differences between wild and cultivated plants suggest either significant alteration of plants through domestication or the provenance of cultivated plants from another region. Indeed, Fosberg et al. (1993) suggest that *G. pictum* may be native to the Moluccas rather than New Guinea.

Hypoestes Sol. ex R.Br.

This genus consists of about 70 species occurring in the tropics and subtropics of the Old World. Two species of *Hypoestes* are known from New Guinea. The count of $n = 15$ (Fig. 3) for *H. floribunda* R.Br., native to Australia and New Guinea, is the first report of a chromosome number for this species. It agrees with most previously reported counts for other species of *Hypoestes* (Daniel and Chuang 1993, 1998).

Using the key to varieties of *H. floribunda* provided by Barker (1986), *Daniel* et al. 6551 would appear to be affiliated with var. *varia* R.M.Barker. This variety was not reported from New Guinea by Barker (1986). *Hypoestes floribunda* var. *neoguineensis* R.M.Barker was reported by Barker (1986) to occur in the same general region of northeastern Papua New Guinea where *Daniel* et al. 6551 was collected. The pubescent filaments and glandular corolla with a tube 8 mm in length and lobes 11 mm in length readily distinguish *Daniel* et al. 6551 from that taxon.

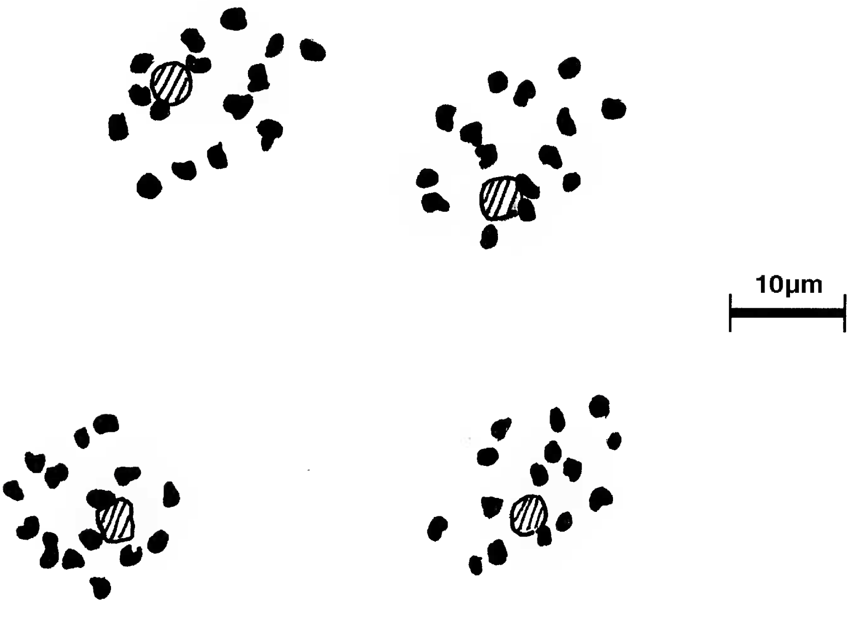

Fig 3. Camera lucida drawing of meiotic chromosome preparation. ***Hypoestes floribunda*** (*Daniel* et al. 6551), late telophase II, n = 15.

The recent report by Daniel and Chuang (1998) of n = 30 for the African species *H. aristata* R.Br. suggests a basic number of x = 15 for the genus. Meiotic complements of n = 15 are also known in both *Dicliptera* Juss. and *Peristrophe* Nees (Daniel and Chuang 1993, 1998), close relatives of *Hypoestes* in Lindau's (1895) tribe Odontonemeae subtribe Diclipterinae.

Jadunia Lindau.

This genus of two species is endemic to New Guinea. Chromosome numbers have not been reported for either of them. Few buds were available for study and only an approximate count of n = ca 16 (Fig. 4A) could be obtained based on a single cell from *J. biroi*. In the preparations from this species, the cytoplasm stained darkly and the chromosomes were not as clearly defined as illustrated.

Jadunia was treated by Lindau (1895) in his subtribe Odontoneminae and he noted affinities with *Calycacanthus*. A chromosome count of n = 16 is noted above for the latter genus.

Lepidagathis Willd.

This genus of 100 or fewer species is mostly paleotropical in distribution. Five species were noted by Höft (1992) as occurring in Papuasia. Previous chromosome counts of n = 9–12, 21, 22, or 42 have been reported for nine species (Daniel et al. 1990, see under *Teliostachya* Nees) of the genus. My counts of n = 21 (Fig. 4B) and n = ca 21 for *L. royenii*, a species known from New Guinea and Queensland, Australia (see Barker 1986), represent the first reports of chromosome numbers for this species. A chromosome number of n = 21 has also been reported for *L. formosensis* C.B.Clarke ex Hayata (Chuang et al. 1963), a species native to Taiwan and the Ryukyu Islands.

Only approximate counts could be obtained for two other collections of *L. royenii*. Because of folded or possibly overlapping chromosomes in the single cells of *Daniel* et al. 6538 and 6609 with nearly countable chromosomes, the exact number of chromosomes (20 vs. 21 or 21 vs. 22 respectively) could not be resolved. In both instances, however, it is likely that 21 bivalents were present. Lindau (1895)

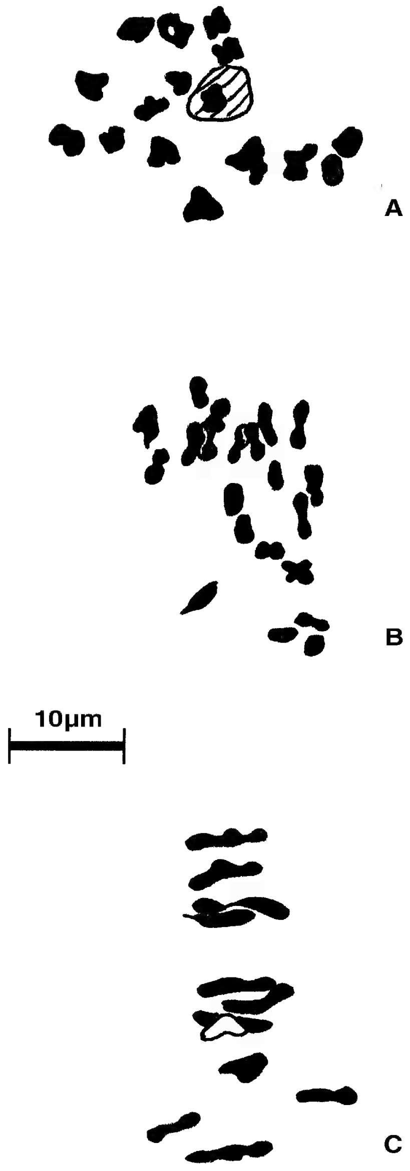

Fig 4. Camera lucida drawings of meiotic chromosome preparation. A. ***Jadunia biroi*** (*Daniel* et al. 6603), diakinesis, n = ca 16. B. ***Lepidagathis royenii*** (*Daniel* et al. 6607), metaphase I, n = 21. C. ***Ruellia repens*** (*Daniel* 6610gh), metaphase I, n = 12.

included *Lepidagathis* in his tribe Barlerieae and Bremekamp (1965) placed the genus "and its nearest allies" into his tribe Lepidagathideae. The only potential relative of *Lepidagathis* for which a chromosome number has been reported is *Barleria*. Daniel et al. (1990) noted that n = 12, 15–21 had been reported for that genus with n = 20 most prevalent. Given the diversity of chromosome numbers so far reported for *Lepidagathis*, the basic number of the genus is not readily evident.

Morphological variation among collections of this species was noted by Barker (1986). Among the collections from which chromosome counts were determined, *Daniel & Forster* 6522 and *Daniel* et al. 6609 have bracts and bracteoles 3–5 mm long with the abaxial surfaces pubescent with two layers of trichomes (a dense layer of glandular trichomes and a subtending layer of eglandular trichomes); *Daniel* et al. 6607 has bracts and bracteoles 6–6.5 mm long with the abaxial surfaces pubescent with three layers of trichomes (an upper layer of eglandular trichomes, a middle layer of sparse glandular trichomes, and a lower layer of eglandular trichomes); and *Daniel* et al. 6538 has bracts and bracteoles 7.5–9 mm long, apically caudate-awned, and abaxially pubescent with three layers of trichomes (as in *Daniel* et al. 6607).

Ruellia L.

In the broad sense in which this genus is often interpreted, it comprises some 250 species occurring worldwide. Höft (1992) noted that 13 species of *Ruellia* are known from Papuasia. A meiotic complement of n = 17 is known for more than 50 species in this morphologically diverse genus (Daniel and Chuang 1998). My count of n = 17 for *R. tuberosa,* native to the West Indies and northern South America and naturalized in New Guinea, agrees with the majority of previous counts for this species (e.g., Grant 1955; De 1966; Verma and Dhillon 1967; Gill 1971; Long 1976; Valsala Deri and Mathew 1982) and for other species of the genus (Daniel et al. 1990). However, occasional reports of n = 16 have been published for *R. tuberosa* (e.g., Sugiura 1936, without citation of voucher; Ellis 1962, without citation of voucher; Subramanian and Govindarajan 1980; Govindarajan and Subramanian 1983, without citation of voucher).

The chromosome number of *R. repens* L., native to southeastern mainland Asia and insular Malesia, is reported here for the first time as n = 12 (Fig. 4C). This number has not been reported previously in *Ruellia* and is the lowest number known for any species of the genus. Recently, Daniel and Chuang (1998) reported n = 24 for the Brazilian species *R. macrantha* (Nees) Mart. ex B.D.Jacks. and the paleotropical species *R. prostrata* Poir. The latter species is morphologically similar to *R. repens* and both are sometimes treated in *Dipteracanthus* Nees (e.g., Bremekamp and Nannenga-Bremekamp 1948). It is increasingly apparent that chromosome numbers in *Ruellia* are somewhat more diverse than previously suspected. Based on chromosome numbers now known for this genus, probable basic numbers for it include x = 12 and x = 17.

Ruellia was treated by Lindau (1895) in his tribe Ruellieae and by Bremekamp (1965) in his subtribe Ruelliinae. Chromosome numbers reported for other genera included in these taxa are n = 25 in *Lankesteria* Lindl. (Mangenot and Mangenot 1962) and n = 15, 17, 19, 21, 22, and 42 (e.g., Grant 1955, Kaur 1970) in *Eranthemum* L.

Thunbergia Retz.

Thunbergia comprises about 100 species native in the Paleotropics. Numerous species are widely cultivated and some have become naturalized. At least three, and perhaps five, species of *Thunbergia* are known from New Guinea. All but one (i.e., *T. papuana* Bremek., which according to Barker (1986) might be synonymous with *T. arnhemica* F.Muell.) appear to be naturalized there. My count of n = 28 for *T. grandiflora* Roxb. (native to southern Asia and apparently introduced and naturalized in New Guinea) agrees with most previous counts for the species (e.g., Daniel and Chuang 1989, 1998; Grant 1955; Kaur 1970, without citation of voucher). Older counts of n = 14 (Nanda 1962, without citation of voucher) and n = ca 14 (Darlington and JanakiAmmal 1945, without citation of voucher) have also been reported for the species. If these latter counts are accurate, then the population I sampled in New Guinea would appear to be tetraploid within the species. Discussions of chromosome numbers in *Thunbergia* were provided by Daniel and Chuang (1989, 1998).

Conclusions

Some of the same chromosomal patterns that were summarized by Daniel and Chuang (1993, 1998) and Daniel et al. (1984, 1990) were observed among Acanthaceae occurring in Papua New Guinea: widely divergent chromosome numbers within a genus (*Ruellia*), dysploidy within a species (*Graptophyllum pictum*), and relatively high (i.e., $n = 14$ or more) haploid numbers for most species. Such chromosomal rearrangements among Acanthaceae have probably led to some of the proliferation in numbers of taxa in this large family.

Four of the genera studied here (*Calycacanthus, Graptophyllum, Hypoestes,* and *Jadunia*) would be included within Bremekamp's (1965) tribe Justicieae subtribe Odontoneminae. The diversity of chromosome numbers encountered among them reflects that reported for other genera of the subtribe from other geographic regions (Daniel and Chuang 1993). Daniel and Chuang (1993) indicated that some of these numbers correlate with other characters and should be useful in recognizing natural groupings within the Odontoneminae. The importance of knowledge of chromosome numbers for discerning systematic relationships among taxa of Acanthaceae has been demonstrated previously (Daniel and Chuang 1993, 1998; Daniel et al. 1984, 1990). Further determinations of chromosome numbers among Papuasian and Australian Acanthaceae should assist in the elucidation of their taxonomy and phylogeny.

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References

Backer, C.A. & Bakhuizen Van Den Brink J.R., R.C. (1965). *Flora of Java*, vol. II. Groningen: N.V.P. Noordhoff.

Bailey, L.H. (1949). *Manual of Cultivated Plants*. New York: MacMillan Publishing Co.

Barker, R.M. (1986). A taxonomic revision of Australian Acanthaceae. *J. Adelaide Bot. Gard.* 9: 1–286.

—— (1996). Additional species, new combinations and other notes on Acanthaceae of Australia. *J. Adelaide Bot. Gard.* 17: 137–152.

Bremekamp, C.E.B. (1965). Delimitation and subdivision of the Acanthaceae. *Bull. Bot. Surv. India* 7: 21–30.

Bremekamp, C.E.B & Nannenga-Bremekamp, N.E.(1948). A preliminary survey of the Ruelliinae (Acanthaceae) of the Malay Archipelago and New Guinea. *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect.* 45: 1–39.

Brummitt, R. (1992). *Vascular plant families and genera.* Kew: Royal Botanic Gardens.

Chuang, T.I., Chao, C.Y., HU, W.W.L. & Kwan, S.C. (1963). Chromosome numbers of the vascular plants of Taiwan. I. *Taiwania* 8: 51–66.

Daniel, T.F. (1995). Revision of *Odontonema* (Acanthaceae) in Mexico. *Contr. Univ. Michigan Herb*. 20: 147–171.

—— (1999). Revision of *Stenostephanus* (Acanthaceae) in Mexico. *Contr. Univ. Michigan Herb*. 22: 47–93.

Daniel, T.F. & Chuang, T.I. (1989). Chromosome numbers of some cultivated Acanthaceae. *Baileya* 23: 86–93.

—— (1993). Chromosome numbers of New World Acanthaceae. *Syst. Bot.*18: 283–289.

—— (1998). Chromosome numbers of cultivated Acanthaceae and systematic implications. *In* Mathew, P. & Sivadasan, M. (eds.), *Diversity and Taxonomy of Tropical Flowering Plants*. Calicut: Mentor Books.

Daniel, T.F., Chuang, T.I. & Baker, M.A. (1990). Chromosome numbers of American Acanthaceae. *Syst. Bot*. 15: 13–25.

Daniel, T.F., Parfitt, B.D. & Baker, M.A. (1984). Chromosome numbers and their systematic implications in some North American Acanthaceae. *Syst. Bot.* 9: 346–355.

Darlington, C.D. & Janaki Ammal, E.K. (1945). *Chromosome Atlas of Cultivated Plants*. London: George Allen & Unwin.

De, A. (1966). Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. I. Cytological Studies. *Trans. Bose Res. Inst.* 29: 139–175.

Ellis, J.L. (1962). Chromosome numbers in some members of Acanthaceae. *Sci. & Cult.* 28: 191–192.

Fosberg, R.F, Sachet, M.-H. & Oliver, R.L. (1993). Flora of Micronesia, 5: Bignoniaceae–Rubiaceae. *Smithsonian Contr. Bot.* 81: 1–135.

Gill, L.S. (1971). Chromosome numbers in certain West-Himalayan bicarpellate species. *Bull. Torrey Bot. Club* 98: 281.

Govindarajan, T. & Subramanian, D. (1983). Karyomorphological studies in South Indian Acanthaceae. *Cytologia* 48: 491–504.

Grant, W.F. (1955). A cytogenetic study in the Acanthaceae. *Brittonia* 8: 121–150.

Hilsenbeck, R.A. (1983). *In* IOPB chromosome number reports LXXX. *Taxon* 32: 505–506.

Hoft, R. (1992). Plants of New Guinea and the Solomon Islands, Dictionary of the genera and families of flowering plants and ferns. *Wau Ecology Institute Handbook* 13: 1–169.

Kaur, J. (1970). Chromosome numbers in Acanthaceae–V. *Sci. & Cult.* 36: 103–106.

Lindau, G. (1895). Acanthaceae. Pp. 274–354 *in* H.G.A. Engler and K.A.E. Prantl (eds.), *Die Natürlichen Pflanzenfamilien* 4 (3b). Leipzig: Wilhelm Engelmann.

Long, R.W. (1976). Biosystematics of *Ruellia tuberosa* L. (Acanthaceae). *Amer. J. Bot.* 63: 951–959.

McDade, L.A. (1984). Systematic and reproductive biology of the Central American species of the *Aphelandra pulcherrima* complex (Acanthaceae). *Ann. Missouri Bot. Gard.* 71: 104–165.

McDade, L.A., Masta, S.E., Moody, M.L. & Waters, E. (2000). Phylogenetic relationships among Acanthaceae: evidence from two genomes. *Syst. Bot.* 25: 105–120.

McDade, L.A., Daniel, T.F., Masta, S.E. & Riley, K.M. (submitted). Phylogenetic relationships among the tribe Justicieae (Acanthaceae): evidence from molecular sequences, morphology, and cytology. *Ann. Missouri Bot. Gard.*

Mangenot, S. & Mangenot, G. (1962). Enquête sur les nombres chromosomiques dans une collection d'espèces tropicales. *Rev. Cytol. Biol. Vég.* 25: 411–447.

Manktelow, M., McDade, L.A., Oxelman, B., Furness, C.A. & Balkwill, M.-J. (in review). The enigmatic tribe Whitfieldieae (Acanthaceae): delimitation and phylogenetic relationships based on molecular and morphological data. *Syst. Bot.*

Nanda, P.C. (1962). Chromosome number of some trees and shrubs. *J. Indian Bot. Soc.* 41: 271–277.

Poivano, M.A. & Bernardello, L.M. (1991). Chromosome numbers in Argentinean Acanthaceae. *Syst. Bot.* 16: 89–97.

Raven, P.H. (1975). The bases of angiosperm phylogeny: cytology. *Ann. Missouri Bot. Gard.* 62: 724–764.

Ridley, H.N. (1923). *The Flora of the Malay Peninsula*, vol. II.London: L. Reeve & Co.

Saggoo, M.I.S. & Bir, S.S. (1982). Cytological studies of certain Acanthaceae from Central India. *Proc. Indian Acad. Sci.* 91: 479–486.

Subramanian, D. & Govindarajan, T. (1980). Cytotaxonomy of some species of Acanthaceae. *J. Cytol. Genet.* 15: 90–92.

Sugiura, T. (1936). Studies on the chromosome numbers in higher plants, with special reference to cytokinesis, I. *Cytologia* 7: 544–595.

Valsala Devi, G. & Mathew, P.M. (1982). *In* IOPB chromosome number reports LXXVII. *Taxon* 31: 773.

Verma, S.C. & Dhillon, S.S. (1967). *In* IOPB chromosome number reports XI. *Taxon* 16: 215–222.